
ADDITIONAL NOTES ON THE
EMBRYOLOGY OF
POLYGONANTHUS
(ANISOPHYLLEACEAE) AND
RELATIONSHIPS OF THE
FAMILY¹

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ABSTRACT

Polygonanthus is reported here to have a *Polygonum*-type embryo sac, like *Anisophyllea* but unlike *Combretocarpus* (with an *Allium*-type embryo sac). This, together with the results of comparisons of other embryological character states reported earlier, indicates an isolated position for *Combretocarpus* within the family *Anisophylleaceae*. On the basis of the available embryological data, we suggest that *Anisophylleaceae* appear to be distinct from both *Rosales sensu stricto* and *Saxifragales*. The family shares many embryological features with *Myrtales* and may be regarded, at least for the time being, as constituting a distinct order in that phylogenetic lineage.

In the course of our earlier study of the embryology of *Anisophylleaceae* (comprising *Anisophyllea*, *Combretocarpus*, *Poga*, and *Polygonanthus*), we were unable to determine several important characters for *Polygonanthus* (Tobe & Raven, 1987a). The collection of an additional sample of *Polygonanthus amazonicus* has made it possible for us to report supplemental embryological results here.

Although we have already discussed the embryology and the floral morphology and anatomy of *Anisophylleaceae* (Tobe & Raven, 1987a, 1988a), our new results, together with the analysis of wood anatomical characters made by Dr. Elisabeth A. Wheeler on the basis of computerized databases and the suggestion by Dahlgren (this volume) that the family belongs in his narrowly defined order *Rosales*, necessitate further analysis. We have, therefore, returned to the question of the relationships of *Anisophylleaceae* in the present paper.

The fixed female flower buds of *Polygonanthus amazonicus* Ducke used in this study were collected by Bruce W. Nelson at Maue, Amazonas, Brazil (voucher *J. L. Zarucchi 3138*, MO) and

fixed in FAA. Microtome sections for observations were made following the standard methods discussed in the previous paper (Tobe & Raven, 1987a).

EMBRYO SAC FORMATION IN *POLYGONANTHUS*

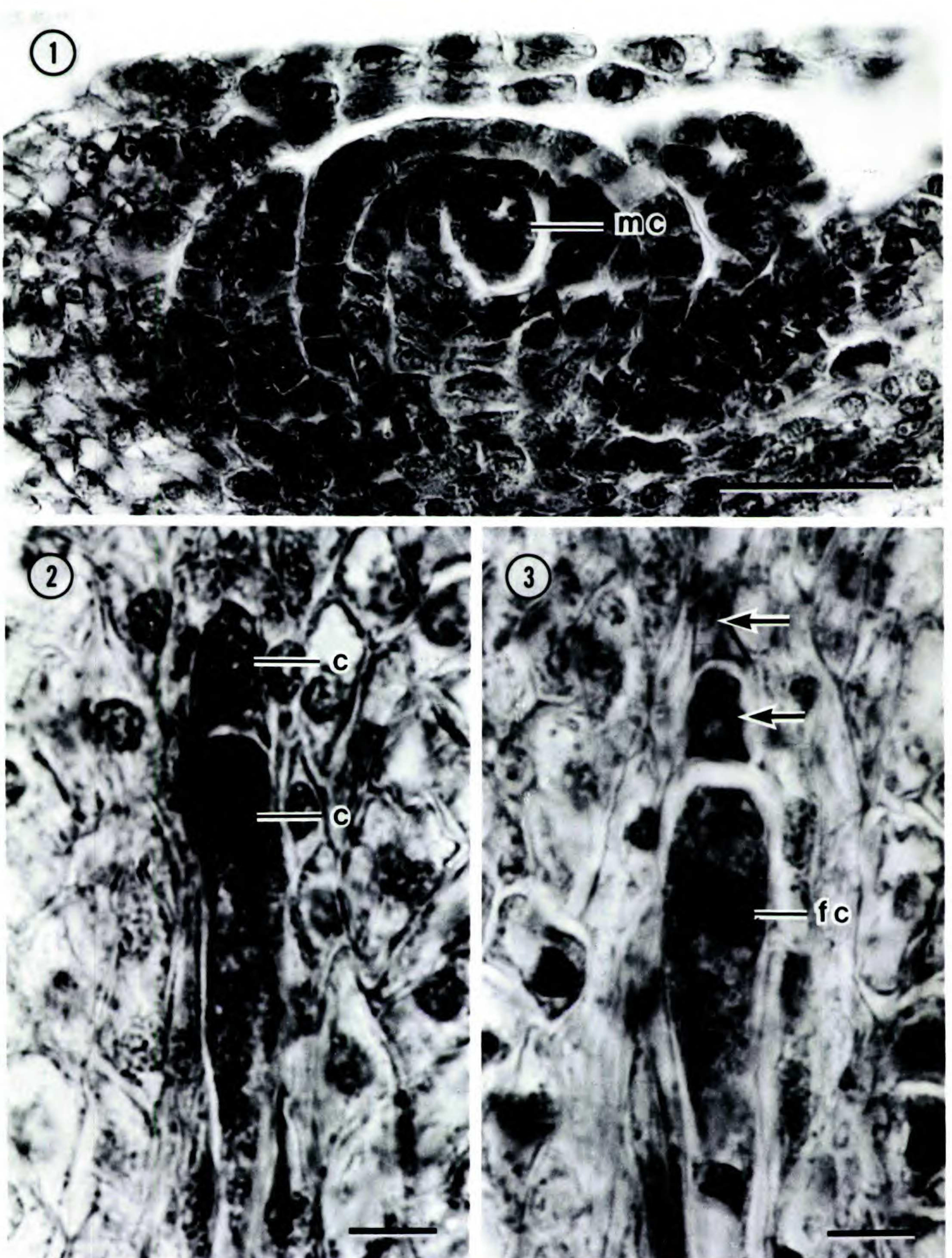
As previously reported, the ovule is anatropous and crassinucellate. At least one parietal cell is observed above a megaspore mother cell, and the occurrence of periclinal cell division in the nucellar apical epidermis is also confirmed (Fig. 1). The megaspore mother cell divides into two cells, with the upper micropylar cell much smaller than the lower chalazal cell (Fig. 2). Subsequent division occurs only in the chalazal cell, giving rise to a triad of megaspores (Fig. 3). Only the chalazal megaspore functions, developing into a monosporic eight-nucleate embryo sac; therefore, embryo sac formation of *Polygonanthus* conforms to the *Polygonum*-type, in agreement with that of *Anisophyllea* but not with that of *Combretocarpus*, which has a bisporic *Allium*-type embryo sac (Tobe & Raven, 1987a).

With respect to other embryological characters,

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FIGURES 1-3. Longitudinal sections of young ovules of *Polygonanthus* showing megasporogenesis.—1. Megaspore mother cell stage.—2. Dyad of megaspores.—3. Triad of megaspores. Abbreviations: mc, megaspore mother cell; c, megaspore; fc, functioning megaspore. Arrows in Figure 3 indicate degenerating megaspores. Scale bars equal 50 μm , 10 μm , and 10 μm , respectively.

Polygonanthus and *Poga* share many plesiomorphies, most of which are common even to *Anisophyllea* (see cladogram in Tobe & Raven, 1987a, fig. 71). In view of these features, the occurrence of *Polygonum*-type embryo sac formation in *Polygonanthus* (also in *Anisophyllea*) indicates an isolated position for *Combretocarpus* within the family. *Combretocarpus* is characterized by many apomorphies, including *Allium*-type embryo sac formation. *Polygonanthus*, like *Poga*, seems to be a relictual genus whose embryological features were mostly inherited from ancestral Anisophylleaceae (Tobe & Raven, 1987a).

RELATIONSHIPS OF ANISOPHYLLEACEAE

We discussed the relationships of Anisophylleaceae (and Rhizophoraceae) earlier (Tobe & Raven, 1987a, b, 1988a), as have other authors in this symposium (e.g., Juncosa & Tomlinson, this volume). Historical views on these relationships are reviewed in these papers, and it seems unnecessary to repeat them here. Instead, we shall use recent suggestions (Tobe & Raven, 1987a, 1988a; Baas, pers. comm.; Dahlgren, this volume) as our point of departure.

Anisophylleaceae have traditionally been assigned to Rhizophoraceae as a subfamily or a tribe. The close resemblance with Rhizophoraceae (particularly with *Carallia*) has been strongly supported by evidence from wood anatomy (van Vliet, 1976; Baas, pers. comm.). Additionally, the result of the computer search by Dr. Wheeler, which incorporated wood anatomical data of about 5,000 dicotyledonous species representing all major and many minor woody genera, confirms that Anisophylleaceae agree completely with *Carallia* and largely with *Crossostylis* and *Gynotroches*; all three of these genera are Rhizophoraceae sensu stricto. In terms of wood anatomy, therefore, Rhizophoraceae undoubtedly agree most closely with Anisophylleaceae, and Baas (pers. comm.) suggested that this evidence rules out many other families as close relatives. Nonetheless, overall evidence from many other lines of investigation, including embryology, makes it absolutely clear that Rhizophoraceae and Anisophylleaceae belong to different evolutionary lines (Tobe & Raven, 1987a, 1988a; Dahlgren, this volume).

What then are their relatives? Dahlgren (this volume) proposed that Rhizophoraceae be placed in Celastrales along with Celastraceae and Elaeocarpaceae, and we agreed with this suggestion on the basis of embryological evidence (Tobe & Raven, this volume). It seems, therefore, to be the

best available hypothesis. Concerning the affinities of Anisophylleaceae, we proposed Myrtales on the basis of embryological evidence (Tobe & Raven, 1987a); in contrast, Dahlgren (this volume) suggested that they belonged in Rosales sensu stricto. On the basis of our analysis (Tobe & Raven, 1988a), Dahlgren concluded that the floral structure of Anisophylleaceae agreed completely with that of Rosales sensu stricto.

Rosales sensu Dahlgren (= Rosales sensu stricto in the following discussion), for comparison with Anisophylleaceae, comprise Crossosomataceae, Rosaceae, Malaceae, Neuradaceae, and Amygdalaceae (Dahlgren, 1983, this volume). Crossosomataceae have often been placed in Dilleniales (e.g., Melchior, 1964; Takhtajan, 1980). On the basis of embryological evidence, Kapil (1970) supported this traditional treatment and rejected the inclusion of Crossosomataceae in Rosales. Despite this, we are not aware of any essential difference in embryological features between Crossosomataceae and Rosaceae, and therefore disagree with Kapil's view. Except for Crossosomataceae, these families are closely related; they are often grouped into a broadly defined family Rosaceae (e.g., Thorne, 1983). Among them, Crossosomataceae, Rosaceae, and Malaceae are relatively well known embryologically, but Neuradaceae and Amygdalaceae are poorly known. The embryological features of Rosales sensu stricto, on the basis of available data, are surveyed in our paper on the embryology of Rhabdodendraceae (Tobe & Raven, 1988b), which is also assigned by Dahlgren (1983) to Rosales sensu stricto. If we compare the embryological features of Anisophylleaceae (see Tobe & Raven, 1987a, for data) with those of Rosales sensu stricto (see Tobe & Raven, 1988b, for data), we find that although Anisophylleaceae share many embryological features with Rosales sensu stricto, the family is distinguished from Rosales sensu stricto in having vascularized integuments, no hypostase, no persistent nucellar tissue in the mature seed, a two-cell-layered thin inner integument (mostly thicker in Rosales sensu stricto), no obturator, and no endosperm in the mature seed. These embryological features suggest strongly that Anisophylleaceae, even though there are some points of similarity to Rosales sensu stricto, do not belong in that order.

We have searched for combinations of embryological features similar to that found in Anisophylleaceae among groups related to Rosales sensu stricto such as Saxifragales sensu Dahlgren. This order comprises 11 families, including several families of "Glossulariineae," a group to which Cronquist (1981, 1983) considered Anisophylleaceae

to belong. We also considered Cunoniales sensu Dahlgren (five families) as possible relatives. We found that Anisophylleaceae are clearly distinct from Saxifragales in lacking the Cellular- or Helobial-type endosperm formation and a persistent endosperm in the mature seed, characteristic features of Saxifragales. As regards Cunoniales, the five constituent families (Cunoniaceae, Baueraceae, Brunelliaceae, Davidsoniaceae, and Eucryphiaceae) are so poorly known embryologically that an adequate comparison with Anisophylleaceae on this basis is not possible at present.

As discussed above, Anisophylleaceae differ strongly from Rosales sensu stricto and Saxifragales in their very different combinations of embryological features. Once more, we emphasize that Anisophylleaceae, on the basis of their embryological features, most closely resemble Myrtales (see Tobe & Raven, 1987a), although Anisophylleaceae do not share the characteristic wood anatomical features of Myrtales (i.e., intraxylary phloem and vested pitting; see van Vliet & Baas, 1984). Myrtales are generally considered to be allied to Rosales(-Saxifragales-Cunoniales) (e.g., Takhtajan, 1980; Cronquist, 1981; Dahlgren & Thorne, 1984). Compared with Rosales sensu stricto and with Saxifragales, Anisophylleaceae and Myrtales apparently share at least one apomorphy, namely, the lack of endosperm in mature seeds. In contrast, Rosales sensu stricto and Saxifragales are apparently more specialized than Anisophylleaceae and Myrtales in other embryological characteristics. For example, in Rosales sensu stricto the inner integument is thicker than the outer one, a feature found only in derived families (Boesewinkel, 1981); and Saxifragales have a Cellular- or Helobial-type endosperm formation, which predominantly occurs in sympetalous groups with a tenuinucellate ovule (Dahlgren, 1975). Therefore, even though the floral morphology of Anisophylleaceae closely resembles that of Rosales sensu stricto(-Saxifragales) (Dahlgren, this volume; see also Cronquist, 1981, 1983), Anisophylleaceae seem, on the basis of their embryological features, to represent a different evolutionary line.

In conclusion, we need further information on the embryology of Rosales sensu stricto and particularly of Cunoniales for more critical comparison. Meanwhile, however, considering evidence of various kinds, it seems appropriate to conclude that Anisophylleaceae, like Myrtales, are one of the derivatives from the common ancestor of Rosales-Saxifragales-Cunoniales. Anisophylleaceae may or may not be directly related to Myrtales, but they do appear to be at approximately the same evo-

lutionary level as that order, at least with respect to embryological features. It might be most appropriate, at least for the time being, to regard Anisophylleaceae as constituting a distinct order in this general phylogenetic lineage.

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